PARENTAL ROLES IN FEEDING NESTLINGS, AND NEST SITES AND NEST SUCCESS IN NORTHERN CARDINALS (*CARDINALIS CARDINALIS*)

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ABSTRACT

PARENTAL ROLES IN FEEDING NESTLINGS, AND NEST SITES AND NEST SUCCESS IN NORTHERN CARDINALS (*CARDINALIS CARDINALIS*)

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Two major aspects of breeding biology were measured for a population of Northern Cardinals in secondary growth habitat at the Aullwood Audubon Center and Farm north of Dayton, Ohio. Nestling feeding rates by both sexes were measured during one hour periods sampled throughout daylight hours, over the first nine days of the nestling period, and over the course of the breeding season, late April to mid-August. Three hypotheses for relative feeding rates by males and females were tested: the equal size, male-biased sex ratio, and bright male hypotheses. Predicted are equal feeding rates, male predominance, and female predominance, respectively. Overall, male cardinals provided 57% ± 13% (n = 12 pairs) of the total trips; the bright male hypothesis is rejected.

Nest sites were characterized and nest success recorded for all active nests throughout the breeding season. Site characteristics measured included nest height, accessibility, visibility, distance to the closest clearing, and tree or shrub species and height. Seven hypotheses predict the position of successful versus unsuccessful nests:

nest concealment, nest height, mid-height, edge distance, nest inaccessibility, needle in a haystack, and rare site hypotheses. The overall success rate was 18% (9 of 50 nests). The probability of success changed over the course of the season; later nests were more successful than early nests. Cardinals built nests proportionately higher in plants as the season progressed. Successful nests tended to be concealed and relatively inaccessible, but not significantly more than unsuccessful nests.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Parental Investment (PI) is defined as any investment by the parent in an individual offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other offspring (Trivers 1972). PI includes the cost of gamete production and parental care. Avian parental care includes the time, energy, and risk involved in the following activities: nest-building, incubation and brooding, defense of offspring, and feeding of nestlings and fledglings.

Parental care is pervasive in the animal kingdom. It occurs in a variety of phyla, notably the arthropods and chordates (fish, amphibians, reptiles, mammals, and birds). In arthropods, female care alone is most common and biparental and uniparental male care are uncommon (Ridley 1978, Zeh and Smith 1985). Indeed, male parental care is exceedingly rare in arthropods other than insects (Zeh and Smith 1985, Tallamy and Wood 1986). Examples of paternal care in insects include male assassin bugs that brood egg masses (Odhiambo 1960) and male giant waterbugs that carry eggs on their backs (Smith 1979). In fish, parental care is apparently absent among chondrichthyan fish (Breder and Rosen 1966, Wourms 1977), while 21% of bony fish families (57% of teleost fish families) show parental care (Breder and Rosen 1966, Gross and Shine 1981, Baylis 1981). Overall, male care is more common than female care (Blumer 1979, Gross and Shine 1981). Care includes such

activities as mouth brooding, ectodermal feeding, and egg fanning (Blumer 1979). In amphibians, biparental care occurs in approximately 20% of the families, male uniparental care in 25%, and female uniparental care in 25% (Gross and Shine 1981). Egg guarding is the most common form of care (Clutton-Brock 1991). In reptiles, male parental care is unknown and female care after egg deposition is rare (Shine 1988a,b). Exceptions to this include female African and Asian cobras that incubate the eggs after they are laid and female crocodilians that provide nests of rotting vegetation to warm the eggs and then carry the newly-hatched young to open water (Neill 1964, Shine 1988a,b). In mammals, the pattern is of female parental care (direct care by the male occurs in less than 5% of all species [Clutton-Brock 1991]), for only females carry the young internally and feed them through lactation. However, males can contribute by indirect means, e.g., protecting and feeding the female. Male care is common among three orders: primates, carnivores, and perissodactyls (Mitchell 1968, Kleiman and Malcolm 1981). For example, foxes and coyotes deliver food to older offspring and male primates carry young and protect them from predators. However, it is not clear whether all male primates carry young for the benefit of the young or for strictly selfish reasons (Strum 1983).

Birds are a unique taxon regarding parental care. There are two extreme forms of development in this group: precocial and altricial (Kendeigh 1952). Precocial young hatch at an advanced state and are nidifugous, while altricial young hatch at an earlier developmental stage and are nidicolous. PI should be higher among altricial species due to a lower investment in eggs compared with precocial

species and a greater amount of postzygotic care (Kendeigh 1952, Ar and Yom-Tov 1978). All passerines are altricial (Kendeigh 1952), which may allow males to be as involved in parental care as are females. Parental behavior is present in virtually all of the approximately 9,000 species of birds (Bock and Farrand 1980), and excluding the brood parasites (80-90 species), the predominant pattern is biparental care (Kendeigh 1952, Lack 1968). Female care alone is found in lek polygynous systems, comprising only 85 species (Welty 1982), while predominant male care (not necessarily male care alone) is found in polyandrous species, comprising at least 27 species (Oring 1986).

Despite the interest in parental care stimulated by Triver's (1972) paper, we lack sufficient data to characterize rigorously parental roles in monogamous, biparental birds (Breitwisch 1989). Further, we do not know whether sexually-selected species within this group differ regarding sex roles from species not displaying the products of sexual selection. Indeed, the mechanism of sexual selection in monogamous species remains enigmatic 120 years after Darwin's seminal contribution.

In this study, I measured nestling feeding rates, a major component of parental investment, in the sexually dimorphic Northern Cardinal (*Cardinalis cardinalis*). The cardinal, a typical passerine, is monogamous and biparental. The predictions of three competing hypotheses for sex roles in feeding rates were tested. In addition, nest success was measured and nest site variables recorded to test the predictions of seven hypotheses for the characteristics of successful nests. The "decision" of where to build

a nest may be one of the most important made by breeding birds, for nest losses to predators are severe (Ricklefs 1969). The overall purpose of this research is to contribute to our understanding of parental care in monogamous, biparental birds.

LITERATURE REVIEW

Morphological Characteristics. The Northern Cardinal (*Cardinalis cardinalis*) is a medium-sized passerine (Family Fringillidae), approximately 20 to 23 cm in length. Males are bright red, and females are buff-brown with tinges of red on the crest, wing, and tail feathers; both have black face masks. Immature cardinals have the same coloration as adult females, with young males having feathers tinged vermillion in varying proportions (Dawson 1903). Furthermore, immatures have blackish bills until 65-80 days of age, when their bills become red-orange like those of adults (Laskey 1944). Females will achieve plumage maturity in their first year, while males will achieve full plumage maturation after their first potential breeding season (Rohwer et al. 1980). Adults of both sexes show plumage variation, although it is not known whether males molt into successively brighter plumages after their first potential breeding season.

The adult cardinal's diet consists of 30% animal matter and 70% vegetable matter, while the diet of cardinal nestlings consists of 95% animal matter and 5% vegetable matter (Bent 1968). Adults eat primarily seeds and wild fruits, while young are fed primarily on beetles, grasshoppers, and caterpillars (Laskey 1944, Bent 1968).

Individual cardinal diets determine plumage phenotype. Carotenoids, responsible for the bright red plumage of male cardinals, cannot be synthesized *de*

novo. They are obtained from dietary sources and are then deposited in the feathers after few biochemical modifications (Brush 1978). Hill (1992) studied the influence of dietary carotenoid level on the amount of red plumage coloration in the house finch (*Carpodacus mexicanus*) in laboratory experiments and found that plumage coloration among males was the result of differential access to carotenoids.

Cardinal nestlings hatch with sparse down feathers. The postnatal molt of the cardinal begins directly after hatching, and takes seven weeks to complete (Wiseman 1977). The postjuvenal molt occurs in September or October and takes 12 weeks to complete (Scott 1967). Postnuptial molts then occur once a year in August or September (Laskey 1944, Scott 1967), producing scarlet plumage with olive-gray feather tips in males. The brighter male plumage is acquired by the loss of these tips in early spring (Bent 1968).

Cardinals can live to six or seven years, with three or four probably the most common length of life (Laskey 1944). Annual survivorship of adults is between 50 and 60% (see Martin and Li [1992] and references therein). During their lifetimes, individuals are not likely to range more than a few miles (Laskey 1944).

Distribution. Cardinals are endemic to North America. Historically, the species range probably was in the southeastern U.S.; from here, the species expanded northward. In 1886, cardinals were only casual north of the Ohio River Valley. However, by 1895 they had extended to the Great Lakes and by 1903 had moved into Michigan (Burns 1963, Bent 1968). By 1910, they were established in southern Ontario and in the southern Hudson River Valley (Bent 1968). Today, the range of

the cardinal extends from southern Ontario and Nova Scotia south to the Gulf Coast and west to the Dakotas and Iowa, and from southern Texas, Arizona, and southern California (introduced to Pasadena in 1923 [Root 1988]) southward into Mexico. Furthermore, the cardinal was introduced in Hawaii in 1929.

River banks and lakeshores probably acted as habitat corridors for the dispersal movements of cardinals during range expansion. Dow (1970) suggested that young birds pioneer new areas via river systems which provide food and cover. Northward movement seems to be hindered by heavy snow cover since cardinals are seed eaters and ground foragers (Dow 1970), while westward movement has been hindered by water availability (Root 1988). The northern edge of the cardinal's range is the "snow belt" of southern Ontario caused by the Great Lakes. Here, grain and cover at farms may aid in allowing cardinals year-round residence. Furthermore, winter feeding has encouraged the cardinal to overwinter in some northern areas (Bent 1968).

Cardinals are a very tolerant species in reference to habitats. They prefer woodland edges, small isolated clumps in open areas, marsh edges, thickets, dry upland shrubs and small tree areas, brushy swamps, gardens, and residential areas with yard shrubbery, fence rows, and hedges (Burns 1963). They are not found in deep forest.

Cardinal populations showed a slight but significant decline in the eastern U.S. over a recent 11 year period [1968-1979], but populations were stable elsewhere. Declines occurred in the southeastern U.S. from Florida north through Tennessee

and Virginia; slight increases occurred from Pennyslvania and New Jersey north into New York and New England where the cardinal is still expanding its range (Robbins et al. 1986). No reasons were given by Robbins et al. for these changes in population size.

Behavior in Non-Breeding Season. The cardinal is a year-round resident in Ohio. During winter, territories from the previous year become home ranges. These home ranges are larger than breeding season territories, and home ranges of neighboring individuals may overlap (Ritchison and Ohmer 1990). The mean maximum home range size for a single individual has been measured as 21.2 ha, with this cardinal spending the majority of its time in only 5.4 ha (Ritchison and Ohmer 1990).

Cardinals flock in groups of six to 25 individuals (Laskey 1944, pers. obs.). Flocks begin to form in late September, during the period of adult molt (Kinser 1973). The flocks are usually fairly even in sex ratio, but sometimes they are male-biased (Laskey 1944).

Flock size will remain approximately constant, but the members in it may change as individuals at the periphery of their home ranges join or leave the group (Laskey 1944, Kinser 1973, Ritchison and Ohmer 1990). Flock size increases with decreasing temperatures (Kinser 1973, Ritchison and Ohmer 1990), possibly due to increased food demands during cold, snowy weather; a greater number of individuals scanning the area for predators and searching for food may allow for more time to forage (Ritchison and Ohmer 1990). Flock size is largest in December, intermediate in November and January, and lowest in February (Ritchison and Ohmer 1990) and

largest in the morning, smaller during the afternoon, and larger again later in the afternoon (Kinser 1973, Ritchison and Ohmer 1990). Seasonal changes correspond with behavioral factors and temperatures, while daily changes may be influenced by periods of active feeding (Ritchison and Ohmer 1990). The periods immediately after sunrise and before sunset may represent periods of active feeding bordering the nocturnal fast.

Flocks are probably composed of young birds that hatched the previous year and some adults that temporarily leave their home ranges for need of food and shelter (Laskey 1944, Ritchison and Ohmer 1990). In these groups, males dominate females, and adults dominate juveniles (Laskey 1944, Ritchison and Ohmer 1990). Adults that join flocks are also often found alone at other times (Ritchison and Ohmer 1990).

The female of a pair may follow her mate through the winter. During this time, the male is dominant to the female and is sometimes aggressive toward his mate. In January and February, he becomes less aggressive (Laskey 1944). During this period, the male begins to establish a territory.

Singing Behavior. Adult cardinals can sing at least 16 common songs, while there may be at least 28 different songs among the males in a single population (Laskey 1944). These songs are known to differ among populations geographically separated (Lemon 1966). Both males and females sing, and their songs are indistinguishable by gender. Males give clear ringing whistles starting in January and February and full song from February through September, while females usually start singing in March

and end in July or August (Laskey 1944). Few, if any, songs are given by either sex in November and December.

Song is used to advertise ownership of a territory and attract females (Lemon 1967). It is also used for pair bonding. Female cardinals sometimes answer songs of males while incubating or brooding, and are also known to "duet" with males during courtship (Laskey 1944). Juveniles begin to warble at three to four weeks of age and use adult phrases within one to two months. By late January and February, song of birds in their first winter is indistinguishable from adult song (Laskey 1944).

Reproductive Behavior. Cardinals are "apparently monogamous" (see Gowaty 1983), biparental passerines. In February, territorial activity begins when males sing high in trees, and many pursuits occur, both male after male and female after female (Laskey 1944). Males establish a territory that includes an open area for foraging (Kinser 1973). Mean territory size ranges from 1.4 ha in Indiana (Kinser 1973) or 1.8 ha in Tennessee to 18.8 ha in Ontario (Dow 1969). By late March, most males have settled on territories (Laskey 1944).

Courtship behavior begins at the end of March or beginning of April. Courtship consists of several aspects of ritualized behavior. First, males and females duet. Second, when perched within a few meters of one another, both sexes may sway their bodies with necks elongated and crests raised. While singing and swaying with neck and crest extended, the male may step down sideways on the limb to the female, after which coition may follow. Third, during the formation of the pair bond, the male feeds the female in courtship feeding. During this feeding, the female

behaves like a juvenile by quivering her wings and begging (Laskey 1944, Bent 1968).

Cardinals are multibrooded and lay up to five clutches in a season, of which four may be brooded successfully (Laskey 1944). The usual clutch size is three eggs early in the season, and two eggs late in the season (Kinser 1973). However, females may lay as many as four or five eggs/clutch (Laskey 1944).

The breeding season is from April through August or September. Cardinals have no decided preference in nesting structures; they have been reported to nest in young evergreens, privet hedges, vines, rose, honeysuckle, hackberry, elm, hawthorn, locust and other species (Laskey 1944, Burns 1963, Bent 1968, Kinser 1973). Nests are usually composed of weed stems, small pliable twigs, bark strips, vines, leaves, and paper (Laskey 1944).

Nests are usually found between one and four meters above the ground, and most between one and one and a half meters (Laskey 1944). Most nests are concealed in twigs and small branches or in mats of vine stems (Laskey 1944). It usually takes three to four days to build a nest, after which there is a three to five day lag before eggs are laid (Laskey 1944, Kinser 1973). Females usually build the entire nest (Kinser 1973), and then lay one egg per day between 0530-0830 hours (Kinser 1973). Eggs are white and are either spotted regularly with bluish, greenish, or grayish tint or irregularly blotched with reddish browns, grays, or lavender (Dawson 1903).

The female alone incubates the eggs. The incubation period lasts 10 to 14 days, and the eggs usually hatch within six hours of one another (Laskey 1944, Kinser

1973). During incubation, the male feeds the female (Laskey 1944, Bent 1968). Once the eggs hatch, the female eats the egg shells (Laskey 1944).

The nestling period lasts seven to 11 days, usually nine to 10 days. During the first half of the nestling period, the female alone broods the young. Cardinal young are altricial. Both sexes feed the young and remove or eat fecal sacs (Laskey 1944, Burns 1963).

The fledgling period lasts approximately five to six weeks, and is divided into three periods (Kinser 1973). The first period is the cryptic phase, when the young are relatively immobile and are dependent on the parents for food and protection. The second period is the free-moving phase, when the young begin to fly throughout the territory and are likely to leave the territory for short periods. Fledglings also begin to forage during this period. The third period is the semi-dependent phase, during which the young become completely independent from the parents. Near the end of the fledgling period, the male cares for the young while the female builds a new nest and begins a new clutch. When incubation is complete and the new eggs hatch, the male chases away the fledglings (Laskey 1944).

The actual importance of male parental care is unclear. Richmond (1978) predicted that females would fledge more, healthier young with the male present during the incubation and nestling stages of a nesting attempt than with the male absent. Males were removed from experimental nests after the females completed test clutches. Comparisons were then made between experimental nests and control nests that had male assistance. Suprisingly, male parental care was not required for

nest success (Richmond 1978). Experimental and control nests had similar predation rates, number of young produced, and nestling weight gains. Furthermore, experimental females did not desert or practice brood reduction more than control females. However, this study did not measure the effects of male removal on female parental care level, number of young produced, nestling weight, or desertion rates in successive broods (with different mates) by experimental females.

Long breeding seasons, rich and predictable food supplies, and high predation rates probably selected for repeated nesting attempts within a season by cardinals. High predation rates may have favored male presence for rapid renesting (Richmond 1978). For whatever historical reasons, cardinals are noteworthy for their renesting potential.

CHAPTER I

PARENTAL ROLES IN FEEDING NESTLING NORTHERN CARDINALS (*CARDINALIS CARDINALIS*)

INTRODUCTION

Parental investment (PI) has been an area of great theoretical interest over the past 20 years. PI patterns by the sexes are thought to be intimately related to reproductive behavior within species and may determine the strength of sexual selection (Trivers 1972). In species of birds where males invest little other than sperm in the offspring and females invest heavily in parental care, females should exert active mate choice. However, most birds are biparental, and both sexes offer a substantial amount of parental care to the offspring.

The connection between PI and sexual selection in biparental birds needs to be clarified. Even though both sexes may invest in the offspring throughout the breeding cycle, PI takes different forms. Investment is measured in terms of the time, energy, and risk in parental care activities along with the energetic cost of gametes. Since these measures are not additive, it remains difficult to predict the relative strength of sexual selection when both parents invest (Burley 1977, Knapton 1984a). It has long been assumed that egg production alone is a major energy cost relative to all forms of male care (Trivers 1972, Wilson 1975, Dawkins 1976). However, this has been challenged recently (Gladstone 1979, Walsberg 1983). The cost of egg production may not mean that females inevitably invest more than males (Knapton 1984a). Furthermore, recent studies have led to the prediction that PI level by males

may be equal to or larger than that of females once all factors have been taken into account, especially in species with male-biased sex ratios (Knapton 1984a, Breitwisch 1989).

The nestling period is probably the most demanding on parental investment, for altricial nestlings grow extraordinarily rapidly, and adults must provision nestlings to allow such growth rates (Breitwisch et al. 1986; however, see Zaias and Breitwisch [1989]). In this study, I assume that any difference in the feeding rate of nestlings by the sexes represents a potential overall difference in parental investment. Furthermore, I assume that males and females do not differ in the number of prey delivered per trip or prey quality (see "Discussion").

Dichromatic species of birds that are biparental and apparently monogamous present an enigma. Their appearance suggests strong sexual selection acting on males, yet their reproductive behavior would not appear to favor intense sexual selection. There are three hypotheses predicting overall PI by the sexes in monogamous, biparental, dichromatic species of birds. First, the "equal investment" hypothesis (Trivers 1972): males and females equally invest in offspring. This hypothesis is based on lack of sexual size dimorphism and assumes that body size is the primary determinant of relative PI. It is equivalent to the null hypothesis for statistical testing. Second is the "skewed sex ratio" hypothesis (Breitwisch 1989). This hypothesis stems from unbalanced adult sex ratios in populations of many birds, with a surplus of males. At all times, there will be males that cannot mate due to a shortage of females. Therefore, females can "demand" extensive parental care from

their mates or divorce them for subsequent nesting attempts with other males that may invest more in offspring. This hypothesis predicts that males will show a higher investment in offspring than will females. Third is the "bright male" hypothesis (Verner and Willson 1969). It has been found that in sexually dichromatic species, a lower percentage of males (44% of 25 species studied) provided at least partial incubation compared with males in monochromatic species (76% of 41 species studied), presumably so that bright males will not attract predators to the nest (Verner and Willson 1969). I extend this argument to the nestling period as a prediction that males in dichromatic species provide little food to the nestlings; male presence is assumed to attract nest predators hunting by visual cues. Therefore, this hypothesis predicts that females will invest more than males in feeding nestlings.

METHODS

Study Site I conducted this study at the Aullwood Audubon Center and Farm, located ca. 15 km northwest of Dayton, Ohio, from May to August 1991. The Aullwood property (39° 52' N and 84° 16' W) is an ca. 80 ha sanctuary with habitats in the following proportions: 26% croplands and orchards, 17% mature woodlands (dominated by beech, *Fagus* spp.; oaks, *Quercus* spp.; maple, *Acer* spp.; buckeye, *Aesculus glabra*), 17% secondary growth (e.g., ash, *Fraxinus* spp.; maple, *Acer* spp.), 16% pasture (European cool season grasses, e.g., alfalfa, *Medicago sativa*), 8% meadow (mixed European forbs, e.g., golden rod, *Solidago* spp.; aster, *Aster* spp.), 5% prairie (native grasses and forbs, e.g., big bluestem, *Andropogon* spp.; Indian grasses, *Sorghastrum* spp.; large-flowered composites, family Asteraceae), 5% residential area (houses, parking lots, and buildings), 2% pine plantings (*Pinus* spp.), 2% wetlands (ponds, marshes, and streams) and 2% wet woods (e.g., ash, *Fraxinus* spp.; red maple, *Acer rubrum*) (J. Ritzenthaler, pers. comm.).

The site is appropriate for this study for several reasons. First, the Aullwood property is permanently protected, ideal for a multi-year study of the behavioral ecology of cardinals. Second, cardinals are known to frequent forest edges, isolated clumps of vegetation in semi-open habitats, marsh edges, and hedges for nesting (Burns 1963). The property represents a reclaimed land parcel managed for diversity

that contains all of these habitats. The cardinal density on this property has been estimated as 30-40 pairs (T. Filliater-Lee and R. Breitwisch, unpubl. data). Third, Aullwood had limited visitation by the public between 06:00 and 10:00 hours, when much of this field work was done.

General Methods I captured cardinals at the end of the non-breeding season (mid-February through mid-March), using mist nets placed near a feeder, and banded them with both USFWS aluminum bands and unique combinations of single colored split-end celluoid bands. Additionally, I captured individuals on territories during the breeding season (mid-March through mid-August). Some males were lured into mist nets using a stuffed male dummy and recorded song playback, although other males were unresponsive to these techniques. Individuals of both sexes were captured with nets set up in known flightpaths used during nestbuilding or used when delivering food during the nestling period.

I banded a total of eight males, seven females, one nestling and one fledgling. I quantified male plumage color using the Munsell Color Chart System (see Appendix A). Too few birds were captured to assess possible correlations between phenotype and level of paternal care.

I found active nests by intensive searches and by quietly following vocalizing individuals. Cardinals give sharp "chip" calls when predators are near their nest or when excited, e.g., when bathing (Lemon 1968), and such calls can sometimes be used to find nests (Montgomerie and Weatherhead 1988). If a nest was discovered while being built, I monitored it almost daily for eggs. After the clutch was complete (or

if the nest was discovered at the egg stage), I monitored it almost daily for hatching. Nests were observed through 10 X 40 binoculars at a distance of 5-15 m, and the nesting stage determined by parental behavior. In general, the approach of the male to the nest site location signaled the hatching of nestlings. When nestlings were present, I collected data on feeding rates beginning on the day of discovery.

I measured nestling feeding rate by each parent for each nest by recording the number of feeding trips by each parent to the nest during one hr periods. I made all observations from a distance of at least five meters away from nests, usually partially hidden by a tree or shrub to avoid disturbing parental activity at the nest. I attempted to record feeding data during at least five hours of nest observations on each pair, with sampling periods scattered thoughout daylight hours (07:00 - 19:00 EST) and on several days distributed over the 10-day nestling period. No data were collected during rainy periods because rainfall may affect female feeding rate due to changes in brooding time (Johnson and Best 1982). I used this time to search for nests until the weather cleared and nests could once again be observed.

Brown-headed cowbirds (*Molothrus ater*) are present on the Aullwood property, and the cardinal is known to be an acceptor host species (Rothstein 1975). Cowbird eggs are difficult to distinguish from cardinal eggs (S.K. Robinson, pers. comm.; see Harrison 1978). Therefore, I did not record the frequency of parasitism in this population. However, I recorded the feeding rate to a single nestling that was identified upon fledging as a cowbird. I assume that the relative feeding rates by the male versus the female of the host pair were not influenced by this nestling being a

cowbird rather than a cardinal. Therefore, due to a small sample size of cardinal pairs with ≥ five hours of data observation, I included this pair in the statistical analysis.

Statistical Testing The sample sizes in analyses are the numbers of pairs of cardinals. All analyses employed non-parametric tests both because sample size is small and underlying distributions of variables are unknown. G-tests were used for tests of associations (e.g., feeding rate versus time of day), and all 2 X 2 tables were corrected due to small sample sizes using Yates' correction for continuity (Sokal and Rohlf 1969). Spearman rank correlations were used for tests of relationship (e.g., feeding rate versus day of nestling life), and all correlation coefficients were corrected for ties. The Wilcoxon signed-ranks matched-pairs test was used for comparing the means of paired data (e.g., male and female feeding rates). Results are reported as significant if they are associated with an *alpha* value of $p < 0.05$. All tests were two-tailed unless otherwise specified, and were performed after data were divided into categories appropriate for sample size.

RESULTS

General I collected nestling feeding data during 87.5 hr of observation on a total of 16 pairs ($\bar{x}$ = 5.5 ± 2.1 hr, range = 1-9). Males provided a mean of 2.0 ± 1.1 feedings/hr (range 1.0 - 5.0), while females provided a mean of 1.4 ± 0.6 feedings/hr (range 0.6 - 2.3).

A summary of the overall feeding rates for males and females in 15 pairs is shown in Fig. 1. One cardinal pair was excluded due to crypticity of the nest; I could not with certainty always identify the individual making a feeding trip. Males fed at an absolutely higher rate on all days except day 6, when females fed more. On day 9, the sexes fed equally; however, the sample for that day includes only 1 pair. The mean number of feeding trips per hr by both parents combined increased slightly but significantly throughout the nestling period (r_s = 0.86, $p < 0.01$, n = 8 days). Females increased their feeding rate slightly over the nestling period (r_s = 0.83, $p < 0.05$, n = 8 days), while males kept their feeding rate relatively constant (r_s = 0.45, $p > 0.05$, n = 8 days). Day 9 was excluded from these analyses because only one pair was sampled.

Four factors may affect mean feeding rates for either or both sexes: (1) time of day, (2) time of season, (3) nestling age, and (4) brood size. Therefore, these factors were tested to determine if they affected feeding rates for either or both sexes. If they do not, then the data may be pooled in testing the sex role hypotheses.

Time of Day Data were collected from 07:00 to 19:00 EST (see Fig. 2). Days were originally divided into four periods: 07:00 - 10:59, 11:00 - 13:59, 14:00 - 16:59, and 17:00 - 19:59. However, small sample sizes within these periods required combination of the last three periods. Therefore, I used two periods, 07:00 - 10:59 ("morning") and 11:00 - 19:00 ("afternoon"). Feeding rates by the sexes were then tested for an association with time of day. To be used in this analysis, a pair had to have been observed for ≥ 2 hr for the time period in question. Values used in this analysis represented the number of individuals of each sex feeding more for the time period. Overall, there was no association between predominance by a sex in feeding and time of day (G_{adj} = 1.63, df = 1, $p > 0.05$). Males in 9 of 11 pairs fed more in the "morning", while males in 4 of 9 pairs fed more in the "afternoon".

Time of season The cardinal breeding season lasted from late April until mid-August in 1991. The first nest discovered failed 7 May during the egg stage, and what was probably the last nest of the season was apparently successful around 16 August. Overall, I collected ≥ 5 hr of data on three nests in May, five nests in June, three nests in July, and one nest in August (see Fig. 3). For each parent in a pair, I calculated the mean feeding rate in trips/hr over the entire nestling period. Feeding rates for each sex were then independently tested for a correlation between time of season and feeding rate. Overall, there was no correlation between either male feeding rate (r_s = 0.12, $p > 0.05$, n = 12) or female feeding rate (r_s = -0.07, $p > 0.05$, n = 12) and time of season.

Nestling Age The nestling period for cardinals in southwestern Ohio lasts approximately 10 days. Data were collected throughout the first 9 days of this period.

For statistical analysis, I divided the nestling period into three 3-day periods reflecting the sigmoidal growth curve of nestling passerines (period 1 = days 1 to 3, period 2 = days 4 to 6, and period 3 = days 7 to 9). Within each period, I counted the number of pairs in which males versus females fed more. Each pair represented had to have been observed for ≥ 2 hr in the 3-day period; if they yielded ≥ 2 hr of data for each 3-day period, they were counted in each one. I then tested for an association between predominance in feeding by a sex and nestling age. Overall, there was no association (G_{adj} = 0.81, df = 2, $p > 0.05$). Males in 5 of 7 pairs fed more in period 1, males in 7 of 10 pairs fed more in period 2, and males in 3 of 6 pairs fed more in period 3 (13 pairs represented).

Brood Size The clutch size of the cardinal averages 3 or 4 eggs (Bent 1968). In this study, I wanted to minimize disturbance near the nest to avoid both female abandonment and predator cuing on sensory information left by human activity (see Gottfried and Thompson [1978] and references therein). Therefore, I checked nests only every third day to count numbers of eggs and/or nestlings. I know brood sizes for only 7 nests: 4 with 3 nestlings and 3 with single nestlings. Males with a brood size of 3 fed a mean of 0.8 ± 0.6 trips/nestling/hr and those with a brood size of 1 fed 1.4 ± 0.3 trips/nestling/hr. Females fed a mean of 0.6 ± 0.2 trips/nestling/hr for brood sizes of 3 and 1.0 ± 0.2 trips/nestling/hr for brood sizes of 1. There was no indication that males responded differently to different brood sizes (Randomization Test for two independent samples, $p >> 0.05$, n = 7). Although there was not a significant association for females, either, there was a trend toward greater provisioning of nestlings in small than in large broods (Randomization Test, p = 0.06,

n = 7).

Time of day, time of season, nestling age, and brood size did not affect male and female feeding rates to nestlings. Therefore, data were pooled in comparing male and female feeding rates.

Male Versus Female Feeding Rate Twelve cardinal pairs had the required ≥ 5 hr of observational data to be used for statistical analysis. Ten of these pairs were used in overall feeding rate analysis because two pairs displayed equal feeding rates and were therefore excluded from analysis (see Siegel 1956). Data from individuals were reduced to mean feeding rates based upon entire nestling periods. Overall, males and females fed at the same rate (Wilcoxon matched-pairs signed-ranks test, T = 11.5, p = 0.11, N = 10 pairs).

Several hypotheses predict relative feeding rates within pairs. Therefore, I also tested for a correlation between male and female feeding trips within a pair, using all pairs with ≥ 5 hr of observational data. I found no correlation between male feeding trips/hr and female feeding trips/hr (r_s = 0.34, p > 0.05, n = 12 pairs) or between male feeding trips/nestling/hr and female feeding trips/nestling/hr (r_s = 0.32, p > 0.05, n = 7 pairs). Therefore, there was no predictability between male and female feeding rates within a pair.

DISCUSSION

Male Versus Female Feeding Rates

Results of this study support acceptance of the null hypothesis (and Trivers' hypothesis): male and female cardinals in the Aullwood population fed nestlings at the same rate. Kendeigh (1952) stated that in the family Fringillidae, females perform most of the nest-building, incubating, and brooding activities while males feed the females and both parents feed the young. Furthermore, he stated that the sexes display approximately equal feeding rates to nestlings. Equal nestling feeding rates have been documented for several other species with altricial young (Purple Martins *Progne subis* [Kendeigh 1952]; Nashville Warblers *Vermivora ruficapilla* [Knapton 1984b]; Northern Mockingbirds *Mimus polyglottos* [Breitwisch et al. 1986]; Western Bluebirds *Sialia mexicana* [With and Balda 1989].

I reject the bright male hypothesis. Brilliant red male cardinals approached the nest and fed nestlings as frequently as cryptically colored females. However, the results may likely support the "skewed sex ratio" hypothesis (predicting that males will invest more in the offspring than females). Males fed at a higher absolute rate on all days except day 6 (see Fig. 1; day 9 was excluded from analysis due to only one pair being represented on that day). These data suggest that males fed nestlings more than did females, but that a larger sample size is required to distinguish

between this hypothesis and the null hypothesis. Furthermore, males may have delivered more prey items per trip or larger prey per trip than did females (see below).

The mean feeding rates to nestlings by males and females combined increased slightly over the nestling period. The female mean feeding rate to nestlings increased over this period while the male mean feeding rate to nestlings stayed relatively constant (see Fig. 1). Feeding rates have been shown to increase over the nestling period in several previous studies of altricial species (Nolan 1978, Pinkowski 1978, Biermann and Sealy 1982, Johnson and Best 1982, Breitwisch et al. 1986). Several hypotheses may explain this pattern. First, females may spend more time brooding and/or shading younger nestlings, decreasing the amount of time available for delivering food to nestlings (Johnson and Best 1982, Carey 1990). Second, as the young grow larger, they require more food to supply sufficient energy for thermoregulation and developmental processes (Biermann and Sealy 1982), and female cardinals may have increased their feeding rates to meet this increased energy demand. Third, females may restore their body condition from depletion resulting from egg production at the beginning of the nestling period (Greenberg and Gradwohl 1983) (however, see Walsberg [1983] for estimation of egg cost).

Within Pair Feeding Rates

There was no relationship between male and female feeding rates within individual pairs. Two hypotheses predict such a relationship, the differential allocation hypothesis (Burley 1988) and the matched quality hypothesis (Breitwisch

1988). The differential allocation hypothesis predicts that mates of attractive individuals are willing to contribute greater than average PI to obtain/or retain their mates. The matched quality hypothesis predicts that mates will contribute equal amounts of PI to the offspring due to either higher quality individuals being more selective of their mates or one sex choosing mates with predictable parental care levels and then matching levels. These two hypotheses predict negative and positive correlations, respectively. No correlation suggests that females may be choosing something other than parental feeding, e.g., prediction of male nest defense level, territory quality, or good genes reflected in behavioral and/or morphological phenotypes.

The null hypothesis is only tentatively accepted for several reasons. First, load sizes and prey quality have not been quantified; once these two important variables are measured for the Aullwood population, parental care levels within pairs may show a correlation (see below). Second, females provisioning at the three highest feeding rates were paired with males provisioning at the three highest feeding rates (four females fed at a rate of 2.3 feedings/hr; the fourth female paired with the tenth ranked male in overall feeding). Although based on few pairs, these results are suggestive of an association, at least in "good feeders". Third, any trend may be masked by an effect of brood size. It has been suggested that as brood size increases, the food requirements per nestling decrease due to decreased thermoregulatory energy requirements (Royama 1966, Johnson and Best 1982). Several studies have shown changes in feeding frequencies for either or both sexes in relation to brood

size (Johnson and Best 1982, Grundel 1987, Carey 1990; however, see Pinkowski 1978 and Breitwisch et al. 1986). I measured nestling feeding rates for seven pairs with known brood sizes (four with three nestlings and three with single nestlings), but found no association with brood size. However, even though the association was not significant for females or males, there was a trend toward females feeding nestlings in small broods more than they fed nestlings in large broods. As in comparing overall male and female nestling feeding rates, a larger sample size is needed to distinguish between these hypotheses for within-pair patterns.

Nestling Feeding Rates and Food Loads

Parental contribution to nestling feeding is not only dependent on feeding rate but also on number and size of prey delivered and prey quality. These other factors need to be taken into account for accurate comparison of male and female nestling provisioning rates (Johnson and Best 1982, Knapton 1984b, Breitwisch et al. 1986). In previous studies measuring various aspects of nestling provisioning for a variety of passerines (Table 1), the general pattern appears to be that the sexes provision nestlings with the same-sized prey and the same number of prey per trip. Where differences exist in the types of prey delivered, there is no indication of a difference in quality of prey. Where differences exist in load size, males deliver larger items than do females. I therefore predict that food load sizes delivered by male cardinals will be at least as big as loads delivered by female cardinals. Load sizes and prey quality need to be measured for male and female cardinals before a rigorous comparison of the equal investment and skewed sex ratio hypotheses can be made.

Cardinals regurgitate food to younger nestlings and carry food in the back of the bill to older nestlings which makes this measurement difficult. However, these factors must also be measured before within-pair hypotheses can be compared rigorously.

Support for Sexual Selection Hypotheses?

In this study, males displayed variation in plumage coloration, although too few males were captured for rigorous analysis (see Appendix A). Furthermore, males showed greater absolute variation in nestling feeding rate (range: 1.0 - 5.0 trips/hr) than did females (range: 0.6 - 2.3 trips/hr). These data suggest the possibility of testing whether male plumage phenotype predicts future parental care level. Variation in both items are necessary, but not sufficient, for sexual selection to act on these traits in males.

Two hypotheses predict female choice of paternal care level via mate choice based on male plumage (Jarvi et al. 1987, Burley 1988). Burley (1988) provided supportive evidence from Zebra Finches (*Poephilia gutatta*) for the differential-allocation hypothesis, while Jarvi et. al. (1987) concluded that the evolution of male secondary sexual characteristics in Pied Flycatchers (*Ficedula hypoleuca*) can be explained, at least in part, by females choosing high quality mates by their conspicuous plumage coloration. Furthermore, Norris (1990) provided evidence for female choice of male plumage coloration, which correlated with the amount of paternal care, in the Great Tit (*Parus major*).

Further research on parental care in Northern Cardinals is warranted to determine if the relative brilliance of the red plumage of males predicts future

paternal care. Male plumage coloration, affected by the amount of carotenoids acquired during molt (Hill 1992), may be an indicator to females of male quality. Plumage brightness may indicate the foraging ability of males, for good foragers should consume higher quantities of carotenoids. Therefore, females choosing brightly colored males may be selecting males who forage well and can therefore continually provide food for nestlings. Furthermore, plumage coloration could be the result of "good genes" if bright males are resistant to parasites (Hamilton and Zuk 1982). Alternatively, male plumage coloration may indicate territory quality (Alatalo et al. 1986, Nagata 1986). These hypotheses await testing for Northern Cardinals.

CHAPTER II

NEST SITES AND NEST SUCCESS IN NORTHERN CARDINALS (*CARDINALIS CARDINALIS*)

INTRODUCTION

Nest site selection may be crucial to the reproductive success of a nesting pair. Lack (1954) estimated that 75% of all eggs and nestlings lost from open cup nesting species are taken by predators. Ricklefs (1969) estimated predation percentages in six passerine species. Overall, predation accounted for 55% of egg losses and 66% of nestling losses. A pair of birds should place their nest in a site where it is not likely to be found by a predator. In the cardinal, it is usually the female that builds the entire nest (Burns 1963, Bent 1968, Kinser 1978). However, males occasionally aid in nest construction (Laskey 1944, pers. obs.). Cardinals renest up to four or five times in a season, and each time the female builds a new nest in a different location on the territory. The female appears to be "responsible" for selecting nest sites (Kinser 1973; however, see Laskey 1944).

I tested predictions of seven hypotheses for the placement of successful versus unsuccessful nests. First, the "nest concealment" hypothesis predicts that nests that are concealed will be more successful than those that are not concealed. This behavior is common among birds; most species of passerines hide their nests, e.g., under leaves or in thick foliage. Second, the "edge distance" hypothesis predicts that nests closer to a habitat edge (defined here as a path ca. 1-3 meters wide or where one habitat changes obviously to another, e.g., forest to pasture) will be less

successful than those placed farther away from an edge. The distance to habitat edge is important because predators including some mammals and birds actively search near these edges. Furthermore, cowbird parasitism increases as one moves from interior forest to forest edge (Brittingham and Temple 1983). Third, the "mid-height" hypothesis predicts that nests placed at mid-height in a tree or shrub will be more successful than those placed either lower or higher in the plant. Nests built higher up may be more easily seen by aerial predators, while those closer to the ground may be located more easily by mammals and snakes. Fourth, the "absolute nest height" hypothesis predicts that nests placed at higher positions will be more successful than those placed lower in the tree or shrub. Nests built high in plant crowns should be concealed better than nests built lower, especially as the season progresses and plants leaf out. Fifth, the "nest inaccessibility" hypothesis predicts that nests that are less accessible will be more successful than those that are more accessible. This hypothesis does not relate to concealment in any way. Inaccessible nests are defined as those nests over water, in thorns, or on the end of thin branches. Sixth, the "needle in a haystack" hypothesis predicts that nests placed in a common species of plant [on the Aullwood property] will be more successful than those that are placed in uncommon plant species. If a predator restricts its search for eggs and nestlings to a few plant species, then nests in the most common plant species will be more difficult to find because there are more plants to search. Seventh, the "rare site" hypothesis predicts that nests placed in uncommon plant species will be more successful than those placed in common plant species. This hypothesis predicts the

opposite of the sixth hypothesis. If a predator searches common species, then it is best to be atypical and nest elsewhere. This hypothesis differs from the others in that success depends on where other members of the species are nesting.

METHODS

Study Site I conducted this study at the Aullwood Audubon Center and Farm, located ca. 15 km northwest of Dayton, Ohio, from May to August 1991. The Aullwood property (39° 52' N and 84° 16' W) is an ca. 80 ha sanctuary with habitats in the following proportions: 26% croplands and orchards, 17% mature woodlands (dominated by beech, *Fagus* spp.; oaks, *Quercus* spp.; maple, *Acer* spp.; buckeye, *Aesculus glabra*), 17% secondary growth (e.g., ash, *Fraxinus* spp.; maple, *Acer* spp.), 16% pasture (European cool season grasses, e.g., alfalfa, *Medicago sativa*), 8% meadow (mixed European forbs, e.g., golden rod, *Solidago* spp.; aster, *Aster* spp.), 5% prairie (native grasses and forbs, e.g., big bluestem, *Andropogon* spp.; Indian grasses, *Sorghastrum* spp.; large-flowered composites, family Asteraceae), 5% residential area (houses, parking lots, and buildings), 2% pine plantings (*Pinus* spp.), 2% wetlands (ponds, marshes, and streams) and 2% wet woods (e.g., ash, *Fraxinus* spp.; red maple, *Acer rubrum*) (J. Ritzenthaler, pers. comm.).

The site is appropriate for this study for several reasons. First, the Aullwood property is permanently protected, ideal for a multi-year study of the behavioral ecology of cardinals. Second, cardinals are known to frequent forest edges, isolated clumps of vegetation in semi-open habitats, marsh edges, and hedges for nesting (Burns 1963). The property represents a reclaimed land parcel managed for diversity

that contains all of these habitats. The cardinal density on this property has been estimated as 30-40 pairs (T. Filliater-Lee and R. Breitwisch, unpubl. data). Third, Aullwood had limited visitation by the public between 06:00 and 10:00 hours, when much of this field work was done.

Methods I discovered nests by intensively searching the study area at least every other day and by following the "chipping" vocalizations of adult individuals (Lemon 1968, Montgomerie and Weatherhead 1988). Nearly all nests were observed daily to record progress. Many nests were observed through 10 X 40 binoculars at a distance of 5-15 m; nestling heads can be detected over the rim of the nest when the nestlings are begging. For nests well concealed in vegetation, parental behavior was observed. In general, the approach of the male to the nest site location signaled the hatching of nestlings.

I recorded nest height and tree or shrub height to 0.1 m using a yardstick where possible and estimating when necessary (nests in dense multiflora rose or higher than several meters). I also estimated distance to the closest clearing to 0.5 m, where "clearing" was defined as either a path ca. 1-3 m wide or where one habitat obviously changed to another habitat, e.g., woodland to pasture. Any nest structures standing alone in a clearing were recorded as in the clearing (distance = 0 m). I recorded nest visibility as whether or not the nest could be seen from approximately six vantage points (above, below, and from four different directions generally related to the four compass directions) using the following classification scheme: "visible" (visible from five or six vantage points), "not visible" (visible from one or two), and

"ambiguous" (visible from three or four). Although this is a subjective categorization, two observers agreed on the visibility classification of all nests.

I noted nest placement using the following categories. First, each nest was classified in one of these four categories: on branches in a tree or bush (stem diameter $\geq$ 1 cm), on twigs in a tree or bush (stem diameter $<$ 1 cm and located distally in plant structure), among cane (*Arundinaria* sp., a woody herb), or in a tree crotch. Additionally, all nests on twigs or branches were recorded as being supported by horizontal or vertical branches. Then, each nest was categorized in one or more of the following locations: below leaves, in thorns, and/or in vines. Any nests located above water were noted with details of the nest placement, e.g., nest in tree with standing water below the entire tree versus nest in tree on the edge of a pond with the nest on the pond side. Finally, I recorded whether the nest was partially supported by a dead fallen branch located underneath the cup of the nest. This variable was added after finding several nests so supported.

I recorded all measurements only after each nest had succeeded or failed, in order to avoid possible disturbance. I recorded the date of success or failure as the first day the nest was found to be inactive, i.e., when eggs or nestlings disappeared in the case of failure or when fledglings were found in the area around the nest in the case of success. Nests discovered inactive after a several day gap in observations were considered inactive at the midpoint of the hiatus. I considered any nest fledging at least one young to be successful.

Brown-headed cowbirds (*Molothrus ater*) are present on the Aullwood property, and the cardinal is known to be an acceptor host species (Rothstein 1975). Cowbird eggs are difficult to distinguish from cardinal eggs (S.K. Robinson, pers. comm.; see Harrison 1978). However, cardinal nestlings are blackish gray with orange skin and red mouth while cowbird nestlings vary from gray and brown to blackish (Harrison 1978). I refrained from approaching active nests to avoid female abandonment of the nest and to avoid attracting predators to the nest. Therefore, I did not record the frequency of parasitism in this population. However, at least one cardinal host pair successfully fledged a single cowbird nestling. I recorded this nest as successful; I am unsure as to how many other nests fledged cowbird young.

I recorded success or failure for all nests. Nests were discovered at various stages in the nesting cycle, and the majority were already at the egg or nestling stage. Such biased discovery can lead to an estimate of nest success for the population higher than the true nesting success (Mayfield 1975). Therefore, I calculated nest-days for the population for three stages: (1) nest-building and egg-laying, (2) egg, and (3) nestling periods. One nest-day represents one active nest for one day, e.g., 12 nest-days represents one active nest for 12 days or 4 nests each active for 3 days, etc. The total number of losses per stage divided by the total number of nest-days in that stage provides a per day mortality rate for each of the three stages recorded here. The mortality rate for the entire period is then calculated by multiplying the mortality rate per day for the period by the length of the period. Additionally, the success rate for the period is calculated as $(1-r)^d$, where r equals the mortality rate

per day and d equals the period in days. To calculate the success rate from nest-building to fledging, the success rates for the three stages are multiplied together.

Statistical Testing All analyses employed the non-parametric G-test for association and the Median Test because the underlying distributions of variables are unknown. All 2 X 2 tables were corrected for small sample sizes using Yates' correction for continuity (Sokal and Rohlf 1969). Results are reported as significant if they are associated with an *alpha* value of $p < 0.05$. All tests were two-tailed unless otherwise specified, and were performed after data were divided into categories appropriate for sample size.

RESULTS

General I found a total of 50 active cardinal nests on the Aullwood property during the 1991 breeding season. Seven nests of these 50 were excluded from analyses, four because of human disturbance and three because their fates were unknown. Therefore, all analyses use sample sizes $\leq$ 43 nests. Overall, 15 nests (35%) were successful and 28 nests (65%) were unsuccessful. However, it is more accurate to use the Mayfield (1975) method in calculating the success rate for the population (see next section).

Survival Rate Nests were found during all stages of the parental care period. The mortality rate for the nest-building and egg-laying period was 0.11 nest failures per nest-day (5 failures/44 nest-days). This period lasts five days, and the survival rate for this period was 0.56 ($= (1 - 0.11)^5$). The mortality rate for the incubation period was 0.06 nest failures per nest-day (16 failures/258.5 nest-days). This period lasts 12 days, and the survival rate for this period was 0.48 ($= (1 - 0.06)^{12}$). The mortality rate for the nestling period was 0.04 nest failures per nest-day (5 failures/131 nest-days). The nestling period lasts 10 days, and the survival rate for this period was 0.66 ($= (1 - 0.04)^{10}$).

Nest success is defined as the survival of at least one nestling to fledging. In this population, the overall success rate for the 1991 season was 32%. If the nest-

building and egg-laying period is included in this calculation, the success rate falls to 18%.

A summary of nesting variables recorded for successful versus unsuccessful nests appears in Table 2. All variables were tested for an association with success versus failure. This table presents the outcome of all statistical tests performed in testing for associations between the nest variable being examined and the probability of success. Descriptive statistics are based on the pooled data on all nests where appropriate.

Before testing hypotheses for nest success versus failure, it is necessary to test for a relationship between probability of success and the date in the season. The first nest of the season was discovered at the end of April and the last nest of the season was discovered in the middle of August. Overall, I discovered four nests in April (none of which were successful), 18 nests in May (four successful), 14 nests in June (seven successful), and seven nests in July (four successful). Nests early in the season were built in April and May, and nests built late in the season were built in June and July. Four of 22 (18%) early season nests were successful, and 11 of 21 (52%) late season nests were successful. Overall, the probability of success was greater later in the season (Median Test; $\chi^2 = 4.13$, df = 1, $p < 0.05$). Similarly, there was a significant correlation between month of the breeding season and probability of a nest being successful ($r_s = 1.00$, $p < 0.05$, $n = 4$), although the samples for April and July are small.

It is possible that one or more nesting variables change over the course of the season. After testing each hypothesis, I also tested for an assocation between the appropriate nest variable and the date in the season. For each test I used the same two categories to represent the date in the season: (1) "early" nests (n = 22), and (2) "late" (n = 21).

Nest Concealment Hypothesis Eighteen nests (42%) were classified as visible, 18 (42%) were classified as not visible, and seven (16%) were ambiguous regarding visibility. In addition, 23 of the nests (53%) were located less than 10 cm below leaves. I ranked nest concealment in five categories from least to most visible: (1) nest not visible and located below leaves, (2) nest not visible but not located below leaves, (3) nest ambiguous with respect to visibility, (4) nest visible but located below leaves, and (5) nest visible and not located below leaves. Originally, category 3 was divided into those nests below leaves and those nests not below leaves. However, due to small sample sizes, all ambiguous nests were pooled for analysis regardless of leaf cover.

There was no association between nest concealment and success of the nest ($G = 2.58$, $df = 4$, $p > 0.05$). Furthermore, there was no association between either "visibility" regardless of leaf cover and probability of success ($G = 0.78$, $df = 2$, $p > 0.05$) or leaf cover regardless of "visibility" and probability of success ($G_{adj} = 0.90$, $df = 1$, $p > 0.05$).

There was also no association between nest concealment and date in the season ($G = 9.49$, $df = 4$, $p > 0.05$), visibility and date in the season ($G = 0.66$,

df = 2, p > 0.05), or leaf cover and date in the season (G_{adj} = 0.60, df = 1, p > 0.05).

Nest Height Hypothesis The mean nest height was 2.2 ± 2.0 m (range = 0.7 - 12 m, n = 43). I tested for an association between nest height and success by dividing all nests into two height categories for the Median Test. Fates of nests in these two categories are shown in Table 3. There was no association between the height of the nest and probability of success (χ^2 = 0.01, df = 1, p > 0.05).

I also tested for an association between nest height and the date in the season. Thirteen of 22 (59%) early season nests were low, and nine of 21 (43%) late season nests were low. There was no association between the height of the nest and date in the season (χ^2 = 0.58, df = 1, p > 0.05).

Mid-Height Hypothesis The mean height of trees and shrubs in which nests were built was 3.7 ± 2.8 m (range: 1.1 - 13 m, n = 43). The height of each nest in the plant (see above) divided by the height of the plant gave the relative height of each nest in the tree or shrub. These ratios were originally divided into the lower, middle, and upper thirds. However, only four nests were classified as being built in the lower third. Therefore, I divided all nests into three approximately equal-sized categories from lowest to highest (see Table 4). There was no association between position in the plant and probability of success (G = 2.57, df = 2, p > 0.05).

I tested for an association between date in the season and the location of the nest in the plant (see Table 4). Cardinals built nests proportionately higher in plants as the season progressed (G = 10.6, df = 2, p < 0.01).

I then tested for associations between different nest placement variables (visibility, success versus failure, and leaf cover) and relative position in the plant for each half of the breeding season. A summary of the associations tested and the test outcomes is shown in Table 5. Middle and high categories were combined for early season nests, while low and middle categories were combined for late season nests since the sample sizes in these cells were too small for analysis if uncombined. Therefore, all statistical tests had 1 degree of freedom. Overall, no nest placement variable was associated with the position of the nest in the plant for either half of the breeding season.

Edge Distance Hypothesis Mean distance from the nearest habitat edge was 2.0 ± 2.2 m (range = 0 - 10 m). Nests were divided into two categories, those closer to the edge (≤ 1.0 m, 24 nests), and those farther from the edge (≥ 1.5 m, 19 nests) for use in the Median Test. There were no nests located between 1.0 and 1.5 m.

Ten of 24 (42%) "close" nests were successful, and five of 19 (26%) "far" nests were successful. There was no relationship between distance from the edge and probability of success of the nest (G_{adj} = 0.53, df = 1, $p > 0.05$). Furthermore, there was no relationship between date in the season and the distance of the nest from the edge (G_{adj} = 0.02, df = 1, $p > 0.05$). Twelve of 22 (55%) early season nests were close, and 12 of 21 (57%) late season nests were close.

Nest Inaccessibility Hypothesis "Inaccessible" refers to any nest located distally on twigs, in close proximity to thorns, over water, or among cane. All other nests were "accessible". Eight of 15 inaccessible nests (53%) were successful, and seven of 28 accessible nests (25%) were successful. There was no association between the

accessibility of the nest and the probability of success (G_{adj} = 2.28, df = 1, p > 0.05). Furthermore, there was no relationship between the proportion of accessible nests and the date in the season (G_{adj} = 0.28, df = 1, p > 0.05). Thirteen of 22 (59%) early season nests were accessible, while 15 of 21 (71%) late season nests were accessible.

Needle In A Haystack and Rare Site Hypotheses Cardinals nested in 16 different plant species on the Aullwood property. The two most common species used were multiflora rose (*Rosa multiflora*) and honeysuckle (*Lonicera* spp.). Appendix B provides a complete listing of the species selected as nest sites during the 1991 breeding season.

The needle in a haystack and rare site hypotheses cannot be tested directly. Predation is rarely observed, and I do not know the major predators of cardinals. Although it is likely that cardinal predators include snakes, small mammals, and predatory birds (Kinser 1973), I do not know whether these predators are restricting their search to a few, commonly used plant species. Further, I did not map the vegetational characteristics of the Aullwood property, and do not know relative abundances of plant species.

However, the four most common species on the Aullwood property are multiflora rose, honeysuckle, ash (*Fraxinus* spp.), and sugar maple (*Acer saccharum*) (John Ritzenthaler, pers. comm.). Therefore, I tested for an association between plant species and probability of nest success. I divided all nests into two categories: those in the four "common" species and those in all other species. Overall, 28 of 41

(68%) nests were built in common species. Two nests of the original 43 nests were excluded from this analysis due to uncertainty about nest plant identification.

Eight of 28 nests in common species (29%) and seven of 13 nests in the remaining species (54%) were successful. There was no association between nesting in common versus uncommon species and probability of success (G_{adj} = 1.45, df = 1, $p > 0.05$). Furthermore, there was no association between use of common species and the date in the season (G_{adj} = 0.01, df = 1, $p > 0.05$). Fourteen of 21 (67%) early season nests were built in common species, while 14 of 20 (70%) late season nests were built in common species.

DISCUSSION

Collias and Collias (1984) stated that in fringillids, the female usually gathers all nesting material and builds the nest while the male accompanies the female to insure against cuckoldry. Furthermore, they stated that in species where sexual dichromatism is marked, females usually build nests without male assistance. In this study, all observed nest-building activities (though few) were performed by females while males closely guarded their mates. The female appears to be responsible for nest-site selection (Kinser 1973, Collias and Collias 1984; however, see Laskey 1944).

Possible Predators

I did not witness any predation events in this study. However, cardinal predators are likely to include snakes, small mammals, and predatory birds (Kinser 1973, Nolan 1978). Rat snakes (*Elaphe obsoleta*), milk snakes (*Lampropeltis doliata*), and Blue Racers (*Coluber constrictor*) have been observed taking cardinal eggs and young in previous studies; all of these species are present on the Aullwood property (B. Grimes, pers. comm.). Snake predators take eggs and/or young and leave the nests undisturbed. This pattern, of nest contents suddenly disappearing with the nest still intact, was common in this population. The eastern chipmunk (*Tamias striatus*) is the only small mammal to date implicated in cardinal nest predation. Predation of one nest in the Aullwood population, found destroyed and with egg shell remains

on the ground near the nest, suggests this predator (Kinser 1973). Possible predatory bird species include blue jays (*Cyanocitta cristata*) and various owls. Similar to snake predation, nests are likely to appear undistubed after predation by birds. However, feathers may be found in the tree of shrub where the nest is located (Kinser 1973).

The brown-headed cowbird (*Molothrus ater*) is an obligate nest parasite that uses Northern Cardinals as a host species (Rothstein 1975). Females sometimes remove host eggs from nests in which they lay eggs, and therefore can be considered a predator of the cardinal. Furthermore, cowbird nestlings hatch earlier, grow faster, and obtain a larger size than host nestlings (Nolan 1978) giving an obvious advantage to the cowbird nestlings in competing with host nestlings. Cowbirds are common at Aullwood and parasitize cardinal nests, among many other host species.

Success Rate for the 1991 Cardinal Population

The success rate for the 1991 breeding season was calculated as 18% via the Mayfield (1975) method. Kinser (1973) also reported a success rate of 18% for a population of cardinals in southern Indiana. Kinser only included nests found before the last egg was laid, but a success rate lower than 18% would likely result if the success rate for his population were recalculated using the Mayfield method. In any field study, it is possible for researchers to leave scent trails followed by olfactorily hunting predators and/or to attract visually hunting predators by approaching nests (Skutch 1976, Nolan 1978). These possibilities probably did not occur in this study, for three reasons. First, in recording nest progress, I simply observed from a distance rather than approach the nest whenever possible. Second, many trails were formed

in searching for and checking the progress of nests. Trails were also formed by Aullwood visitors and staff members. These many trails would have seldom rewarded predators following visual or olfactory cues (Nolan 1978). Third, many nests were located by searching areas of cardinal activity. During these searches, it is likely that nests well-concealed and therefore missed by human observers were also missed by at least some visually seeking predators (Skutch 1976).

Cardinal nests built later in the breeding season were more successful than earlier nests. Other studies have shown this same pattern (Best 1978, Kinser 1973, Nolan 1978). There are two reasons why success may depend of the date in the season. First, snakes may be less active in midsummer, and this decrease in activity due to hot weather may be accompanied by a decrease in food intake (Kinser 1973, Nolan 1978; however, see Best 1978). Second, cowbird parasitism has been shown to decrease dramatically in June and July (Best 1978, Nolan 1978). The only nest placement variable changing with date in the season was the relative height of the nest in the plant. Snakes hunt from the ground, and cowbirds may choose nests located higher in plants (Nolan 1978). Therefore, nests closer to the ground may be more susceptible to snake predation and nests higher in the plant may be more susceptile to cowbird parasitism. As the season progresses and plants leaf out, females may place nests higher in shrubs for concealment (Collias and Collias 1984), yet low enough to decrease parasitism frequency.

In general, birds in populations nesting early in the season have a low probability of successfully fledging young (see Price et al. [1988] and references

therein). However, there are several advantages to cardinal pairs that manage to nest successfully early in the season. Females lay three eggs/clutch early in the season as opposed to two eggs/clutch later in the season (Kinser 1973), therefore larger clutches may result in larger broods. Furthermore, fledglings produced early in the season may be more likely to survive to reproductive age than those produced later (Nolan 1978).

Nest Placement

Species Chosen The majority of all nests (70%) were placed in honeysuckle, multiflora rose, or in an aggregation of plants including one of these two species (see Appendix B). These two species are among the most common on the Aullwood property (J. Ritzenthaler, pers. comm.) and appear to offer concealment and protection. Furthermore, female cardinals may decrease predation risk if they nest in the most common plant species (the "needle in a haystack" hypothesis) and if major predators search only a few species for nests.

Distance to Edge Cowbirds parasitize nests closer to clearings more frequently than nests farther from openings (Brittingham and Temple 1983), while some predators select habitat edges for foraging (Gates and Gysel 1978). However, although not significantly different, successful nests tended to be closer to habitat edges than unsuccessful nests (see Table 2). Cardinals may nest close to paths because human activities decrease the number of predators in these areas (Collias and Collias 1984). The Aullwood Audubon Center and Farm conduct tours for school children throughout the property (pers. obs.); these groups may discourage predators from

searching near the trails and in other areas frequented by these groups.

Nest Concealment and Accessibility Surprisingly, nest inaccessibility and concealment did not increase the probability of success (see Table 2). Most small birds hide their nests in vegetation and/or place nests in locations that are inaccessible to some predators (Collias and Collias 1984). A more rigorous classification system for these two variables may be required to reveal any differences between successful and unsuccessful nests. In addition, a larger sample size would allow use of multi-dimensional G-tests of association, which can assess interactions between variables (M. Rayle, pers. comm.; see Colgan and Smith 1978). Females select nest sites based on several variables, including security from predators and shelter from the physical environment (Collias and Collias 1984), and there is little reason to believe that any single variable related to nest site is responsible for nest success. Perhaps further work on nest success and nest placement variables with the Northern Cardinal will reveal nest placement strategies leading to successful nests.

APPENDICES

Appendix A: Male Plumage and Bill Color Scores

Method of Scoring. Male plumage colors were scored using the Munsell Color Chart System. Plumage colors were quantified on the upper breast, head crest, and wing feathers and on the bill. Each body region was recorded as a three number code referring to the hue, value, and chroma of the Munsell paint swatch most closely resembling the color of the region being examined.

Hue refers to the quality of the color (purple-red, red, red-yellow, etc.) and the number with the hue corresponds to where the color falls in each hue; red was the only hue used in this study. Lower numbers in the red range are close to red-yellow while higher numbers in the red range are close to purple-red. Value refers to the amount of black in the paint swatch. Lower value numbers correspond to dark colors and higher value numbers correspond to light colors. Chroma refers to the purity or intensity of the color. Lower numbers represent very little color in the swatch and higher numbers refer to nearly pure coloration in the swatch.

Each male received a three number code (for hue, value, and chroma) for each of the four body regions measured. Then, the male was assigned an overall score for each body region (see Hill [1990] and Muma and Weatherhead [1989]). Each of the numbers of the code was assigned a score (Table A1), and the three scores for that particular Munsell swatch were summed to provide an overall score

for that body area (Table A2). For example, the color swatch 7.5R 4/8 would be assigned a score of 3 (=1+1+1) (Table A1). In this scoring system, higher hue, value, and chroma scores correspond to brighter plumage. Therefore, in the previous example, a score of 3 would represent the dullest color for a male cardinal, while a score of 12 (i.e., 10R 6/18) would represent the brightest color.

Table A1. Scoring scheme for male Northern Cardinals captured during the 1991 and early 1992 breeding seasons. This scoring system is based on Hill's (1990) method.

HUE	SCORE
7.5R	1
8.75R	2
10R	3

VALUE	SCORE
4/	1
5/	2
6/	3

CHROMA	SCORE
/8	1
/10	2
/12	3
/14	4
/16	5
/18	6

Table A2. Male Northern Cardinal plumage and bill rankings for the 1991 and early 1992 breeding seasons. Rankings refer to Munsell Notation (see text for details). *Males are from the early 1992 breeding season.

MALE #	BODY REGION	COLOR RANKING	SCORE
410	Upper Breast	8.75R 4.5/16.5	8.75
	Head Crest	8.75R 4.5/16.5	8.75
	Wing	7.5R 5/10	5
	Bill	10R 6/12	9
411	Upper Breast	8.75R 5/16	9
	Head Crest	8.75R 5/16	9
	Wing	7.5R 5/10	5
	Bill	7.5R 6/12	7
413	Upper Breast	7.5R 5/16	8
	Head Crest	7.5R 5/16	8
	Wing	7.5R 5/10	5
	Bill	8.75R 6/12	8
414	Upper Breast	8.75R 5/14	8
	Head Crest	8.75R 5/16	9
	Wing	7.5R 4/10	4
	Bill	8.75R 6/14	9
416	Upper Breast	7.5R 6/16	9
	Head Crest	7.5R 4/12	5
	Wing	7.5R 5/10	5
	Bill	8.75R 6/12	8
417	Upper Breast	8.75R 5/15	8.5
	Head Crest	7.5R 5/14	7
	Wing	7.5R 5/10	5
	Bill	7.5R 5-6/12	6.5

Table A2. Continued.

MALE #	BODY REGION	COLOR RANKING	SCORE
418*	Upper Breast	8.75R 4/14	7
	Head Crest	7.5R 4/12	5
	Wing	7.5R 4/10	4
	Bill	7.5R 5/12	6
419*	Upper Breast	8.75R 4/14	7
	Head Crest	7.5R 4/12	5
	Wing	7.5R 4/8	3
	Bill	8.75R 5/12	7
421*	Upper Breast	7.5R 5/14	7
	Head Crest	7.5R 4/12	5
	Wing	7.5R 4/10	4
	Bill	8.75R 5/12	7
423*	Upper Breast	7.5R 4/16	7
	Head Crest	7.5R 4/12	5
	Wing	7.5R 4/8	3
	Bill	8.75R 5/12	7

Appendix B. Plant species chosen for nesting by Northern Cardinals in 1991.	
Species	# Nests
NESTS IN SINGLE PLANT SPECIES:	
Honeysuckle, *Lonicera* spp.	14
Multiflora rose, *Rosa multiflora*	13
Red cedar, *Juniperus virginiana*	2
Locust, *Robina pseudoacacia*	1
Cane, *Arundinaria* sp.	1
Paw paw, *Asimina* sp.	1
Wild grape, *Vitis rotundifolia*	1
Slippery elm, *Ulmus rubra*	1
Dogwood, *Cornus* sp.	1
Hawthorn, *Crataegus* sp.	1
Pine, *Pinus* sp.	1
Cherry, *Prunus* sp.	1
Climbing bittersweet, *Celastrus* sp.	1
NESTS SUPPORTED BY TWO OR MORE PLANT SPECIES:	
Honeysuckle, Wild grape, Unknown vine	1
Multiflora rose, Wild grape	1
Honeysuckle, Multiflora rose	1
Multiflora rose, Wild grape, Virginia creeper (*Parthenocissus quinquefolia*)	1
Honeysuckle, Wild grape	1
Wild grape, Elm	1
Cherry, Wild grape	1

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Table 1. Summary of food load data collected on various passerines. Feeding rates were either equal (=), male-biased (M), or female-biased (F). Prey size and # of prey were similar for both sexes (=), or males delivered larger prey/more prey per trip (M), or females delivered larger prey/more prey per trip (F).

SPECIES	FEEDING RATE	PREY SIZE	# OF PREY/TRIP	PREY TYPE*	REFERENCE
Tree Swallow	=	=	NO DATA	NO DATA	Quinney 1986
Prairie Warbler	F	= or M**	=	SAME	Nolan 1978
Yellow Warbler	M	M	=	DIFFERENT	Biermann and Sealy 1982
Nashville Warbler	=	=	=	SAME	Knapton 1984
Mountain Chickadee	M	M	=	NO DATA	Grundel 1987
Field Sparrow Brood Size 1 or 2 Brood Size 3 or 4	 F M	 = M	 F M	 NO DATA NO DATA	Carey 1990
Eastern Bluebird	F	NO DATA	NO DATA	DIFFERENT	Pinkowski 1978
Northern Mockingbird	=	=	NO DATA	SAME	Breitwisch et al. 1986
Dot-Winged Antwren	=	= or M***	NO DATA	DIFFERENT	Greenberg and Gradwohl 1983

* "Different" prey types, but no indication of quality.

** Males generally brought in larger prey items, however, no statistical test performed.

*** Pairs were analyzed separately; in 3 of 8 pairs males delivered larger prey items.

Table 2. Summary of nesting variables for Northern Cardinal nests during the 1991 breeding season. Variables that were not significant were combined and the range of the variable recorded in the fourth column of the table.

VARIABLE	SUCCESSFUL NESTS (n=15)	UNSUCCESSFUL NESTS (n=28)	OVERALL** (n=43)	SUCC. VS UNSUCC. STATISTICAL TEST
Tree Height	4.6 ± 3.6 m	3.2 ± 2.1 m	3.7 ± 2.8 m (1.1-10 m)	Median Test, NS
Nest Height	3.0 ± 3.1 m	1.7 ± 0.6 m	2.2 ± 2.0 m (0.7-12 m)	Median Test, NS
Proportionate Height	0.7 ± 0.2 m	0.6 ± 0.2 m	0.6 ± 0.2 m (0.1-0.9 m)	G-Test, NS
Edge Distance	1.4 ± 1.6 m	2.3 ± 2.4 m	2.0 ± 2.2 m (0-10 m)	Median Test, NS
Species Chosen	6 in common 7 in other	20 in common 8 in other	26 in common 15 in other	G-Test, NS
Visibility	11 visible 2 ambiguous 5 not visible	8 visible 5 ambiguous 12 not visible	19 visible 7 ambiguous 17 not visible	G-Test, NS
Leaf Cover	10 under leaves 5 without leaves	13 under leaves 15 without leaves	23 under leaves 20 without leaves	G-Test, NS
Concealment*	4 in category 1 1 in category 2 2 in category 3 4 in category 4 4 in category 5	7 in category 1 5 in category 2 5 in category 3 3 in category 4 8 in category 5	11 in category 1 6 in category 2 7 in category 3 7 in category 4 12 in category 5	G-Test, NS
Accessibility	7 accessible 8 inaccessible	21 accessible 7 inaccessible	28 accessible 15 inaccessible	G-Test, NS
Date in Season first half second half	 4 11	 18 10	 22 21	Median Test, $p < 0.01$

* See text for explanation of categories.
** Range is represented in parentheses.

Table 3. Nest heights and nest success for Northern Cardinals during the 1991 breeding season. Nest heights are categorized for the Median Test (see text).

CATEGORY	NEST HEIGHT RANGE	# OF NESTS	# SUCCESSFUL
Low	0.7 - 1.5 m	22	8 (36%)
High	1.7 - 12.0 m	21	7 (33%)

Table 4. Proportionate height and nest success for Northern Cardinal nests during the 1991 breeding season. Nest locations were categorized by dividing nests into three approximately equal-sized groups (see text).

LOCATION	RANGE	# OF NESTS	DATE IN SEASON EARLY	LATE	TOTAL # SUCCESSFUL
Low	0.13-0.50	15	12	3	5 (33%)
Middle	0.58-0.78	14	7	7	3 (21%)
High	0.80-0.93	14	3	11	7 (50%)

Table 5. Associations between leaf cover, visibility, and success in relation to relative position in the plant for each half of the Northern Cardinal 1991 breeding season. No association was significant (see text).

VARIABLE	DATE IN SEASON	
	EARLY (n=22)	LATE (n=21)
Leaf Cover	$G_{adj} = 1.16$	$G_{adj} = 2.36$
Visibility	$G_{adj} = 1.67$	$G_{adj} = 0.05$
Success	$G_{adj} = 0.13$	$G_{adj} = 0.42$

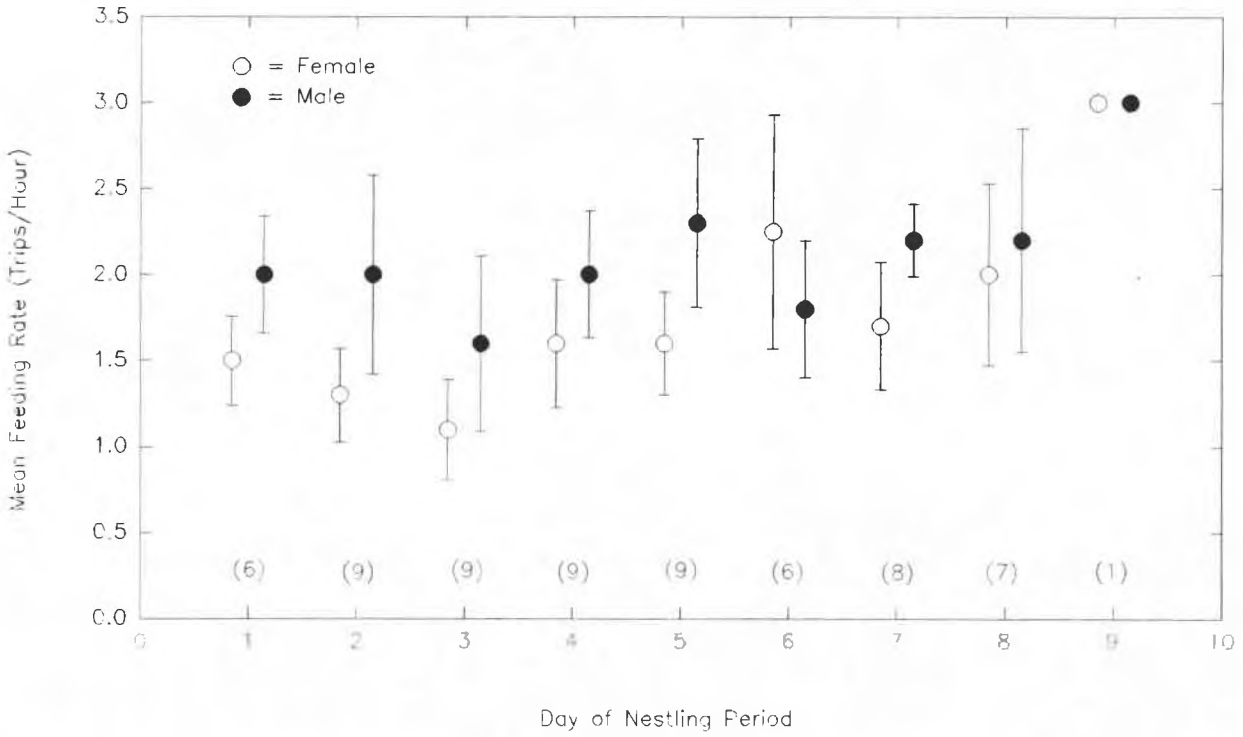

Fig. 1. Male and female Northern Cardinal feeding rates to nestlings during the first 9 days of the nestling period during the 1991 breeding season. Overall, 15 pairs are represented. Numbers in parentheses correspond to the number of pairs with at least one hour of data for the day. Day 0 represents hatching, and day 10 represents fledging. On day 9, the male and female fed at the same rate. Circles represent means, and bars represent standard errors of the mean.

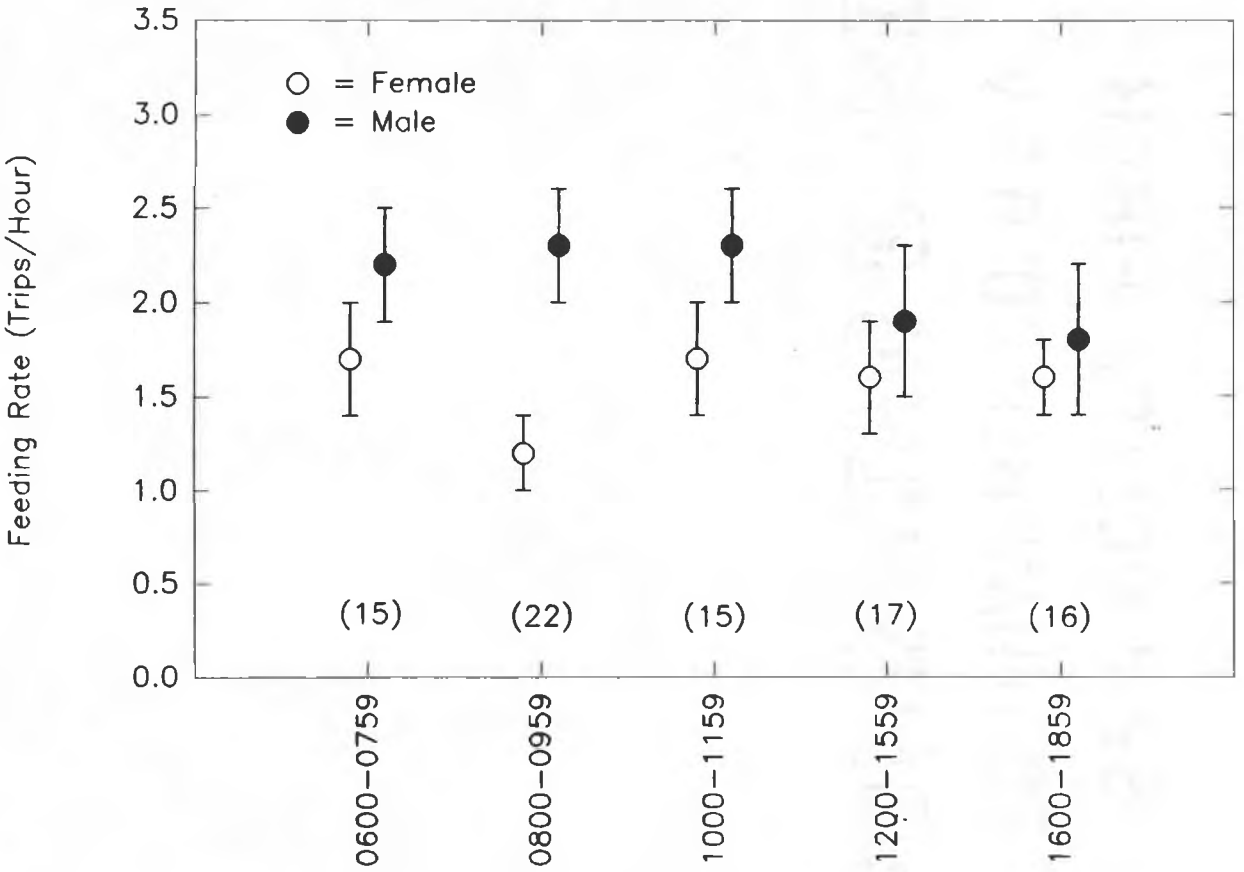

Fig. 2. Male and female Northern Cardinal feeding rates to nestlings related to time of day during the 1991 breeding season. Sixteen different pairs are represented, with the overall mean feeding rate for each period represented. Bars represent standard errors of the mean. Numbers in parentheses represent the number of hours of observations for each time period.

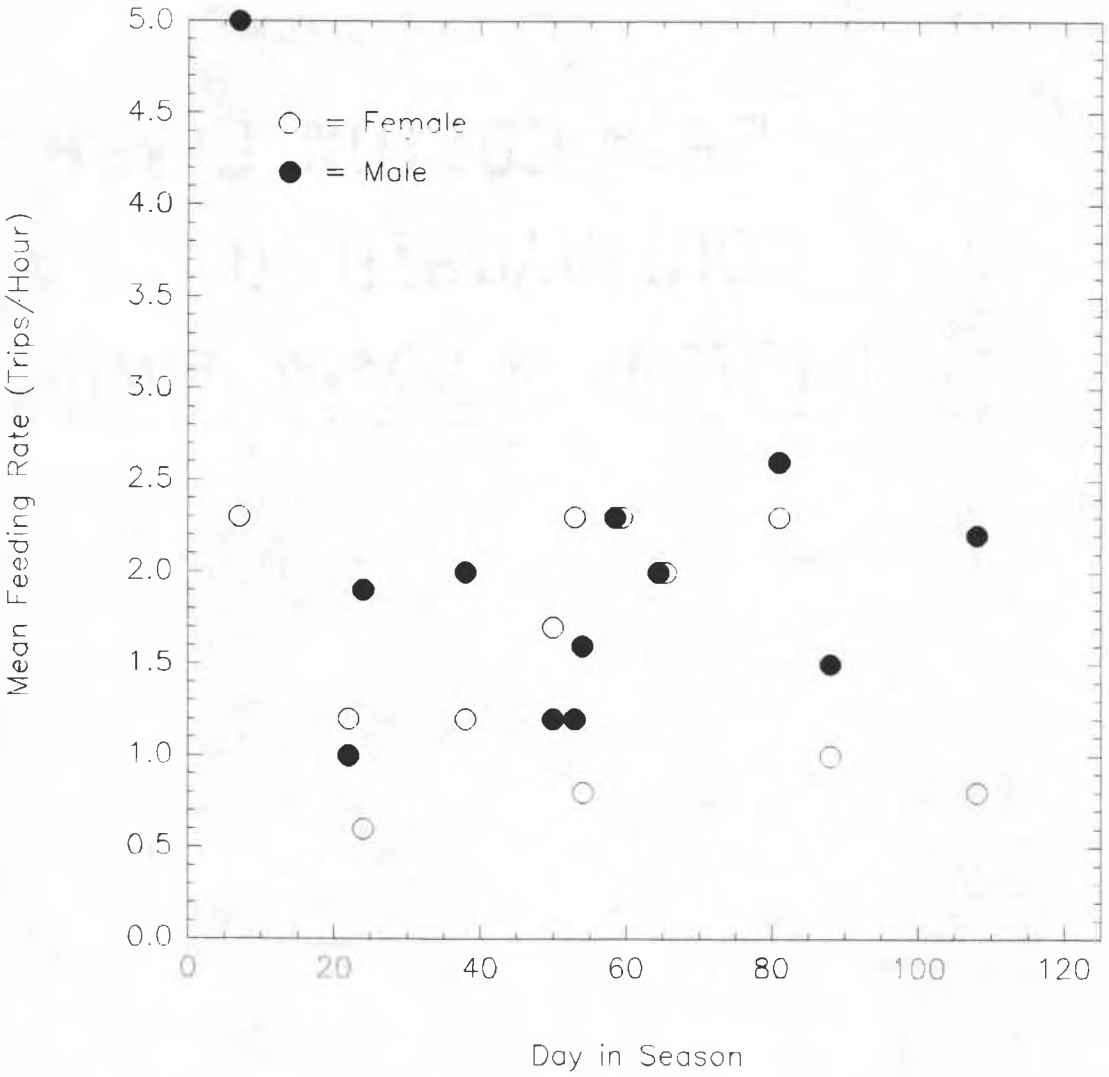

Fig. 3. Male and female Northern Cardinal feeding rates to nestlings related to date in the 1991 season. Day 0 = May 1, day 32 = June 1, day 62 = July 1, and day 93 = August 1. Twelve different pairs are represented, with their mean feeding rate over the entire nestling period plotted on the date of the first day of nestling life.